

Hemispheric Difference in Human Skin Color

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ABSTRACT Previous studies of human skin color have shown a strong relationship between skin color and distance from the equator, which has been interpreted as a link between skin color, latitude, and the intensity of ultraviolet radiation. The underlying assumptions are that UV radiation is greatest at the equator and that it diminishes with increasing latitude to the same extent in both the Northern and Southern Hemispheres. The standard analysis of human skin color is based on these assumptions, such that skin color is assumed to be darkest at the equator, and the decrease of skin color with latitude is assumed to be the same in both hemispheres. A nonlinear piecewise regression model was developed to test these assumptions and applied to mean skin reflectance data from 102 male samples and 65 female samples from across the Old World. For both males and females, skin reflectance (%) is lowest at the equator (darkest skin). Among males, skin reflectance increases roughly 8.2% for every 10 degrees of latitude in the Northern Hemisphere but only 3.3% for every 10 degrees of latitude in the Southern Hemisphere. Among females, the corresponding numbers are 8.1% in the Northern Hemisphere and 4.7% in the Southern Hemisphere. These results indicate that human skin color is darker in the Southern Hemisphere than in the Northern Hemisphere at equivalent latitude. Recent research shows that UV radiation is higher in the Southern Hemisphere than in the Northern Hemisphere at similar latitude. This difference, relating to astronomical and climatic conditions, may have existed in the past at different times and perhaps influenced the evolution of human skin color. *Am J Phys Anthropol* 104:449–457, 1997.

The geographic distribution of human skin color is perhaps one of the best examples of natural selection resulting in a strong relationship between phenotype and environment. It has long been recognized that human skin color is darkest near the equator, and lighter with increasing distance from the equator (Loomis, 1967; Blum, 1969; Roberts and Kahlon, 1976; Tasa et al., 1985). Early attempts to present this relationship graphically were flawed by the use of subjective measures of skin color, including visual observation and color tile matching (Byard, 1981). The study of human skin color advanced in the 1950s (Weiner, 1951) with the use of portable abridged reflectance spectro-

photometers that provided an objective measure that is not affected by observer error (Lees et al., 1978). Skin color is measured as the percentage of light reflected back from unexposed skin at a given wavelength.

To date, anthropological studies have provided skin reflectance data for a substantial number of human populations. Several comparative analyses have demonstrated a high correlation between skin reflectance and

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distance from the equator (e.g., Roberts and Kahlon, 1976; Tasa et al., 1985). These correlations suggest a strong geographic correspondence between human skin color and ultraviolet (UV) radiation. While a variety of hypotheses have been proposed explaining a link between UV radiation and skin color (Byard, 1981; Robins, 1991; Frisancho, 1993), the basic geographic relationship has been accepted by all workers.

The most common approach when analyzing the geographic distribution of human skin color has been to take distance from the equator (the absolute value of latitude) as the independent variable (Roberts and Kahlon, 1976; Tasa et al., 1985). This approach seems reasonable given the suggestion that UV radiation is greatest at the equator and decreases with distance from the equator. Although reasonable, the underlying regression model actually assumes rather than tests, the hypothesis that human skin color is darkest at the equator. The model also assumes that the relationship between skin color and latitude is the same in both the Northern and Southern Hemisphere. This assumption may not be valid: today, at least, UV radiation levels are higher in the Southern Hemisphere than in the Northern Hemisphere at equivalent latitudes (McKenzie and Elwood, 1990; McKenzie, 1991; Seckmeyer and McKenzie, 1992). If hemispheric differences in UV radiation also occurred at times in the past that were critical in the evolution of skin color, then hemispheric differences in skin color would result.

The purpose of this paper is to examine the geographic distribution of human skin color in the Old World by using a nonlinear regression model that allows two assumptions to be tested: 1) human skin color is darkest at the equator, and 2) the slope of human skin color versus latitude is the same in both the Northern and Southern Hemispheres. Application of this model to comparative data shows that while the first assumption is valid, the second is rejected. Human skin color is darker in the Southern Hemisphere than in the Northern Hemisphere at equivalent latitude. The hemispheric difference in human skin color may

reflect hemispheric differences in UV radiation.

MATERIALS

The available literature on human skin color was surveyed to find as many samples of reflectance data as possible. Several restrictions in data collection were applied to obtain the final sample. Data collection was limited to Old World samples. Most skin reflectance studies in the Old World have relied on the EEL reflectometer, whereas most New World studies have used a Photovolt reflectometer (EEL and Photovolt are manufacturers' names). While similar in function, readings from the two machines are not directly comparable because of different wavelengths and transmission properties. While several studies have attempted to develop conversion formulae between the two machines (Garrard et al., 1967; Lees and Byard, 1978; Lees et al., 1979), they have not been developed (or validated) on sufficient numbers of populations to warrant their use in the present study. While there are many Old World studies using the EEL machine, there are only a small number of New World samples that have used this machine.

Data collection was limited to reflectance readings taken on a single filter (EEL filter number 609), which corresponds to 685 nm. Analysis was confined to this single filter because it maximizes populational differences in skin reflectance and is available for the maximum number of studies surveyed. Almost all skin reflectances were taken at the relatively unexposed upper inner arm site to minimize environmental effects. The one exception was Barnicot's (1958) Nigerian study which used the lower inner arm site. Preliminary analysis suggested no noticeable bias, and this study was included in the final data set.

Admixed samples (e.g., European-Indian hybrid studies) were excluded. In inheritance studies, where both parent and offspring data were reported, only the parental data were used. Other than that, no attempt was made to control for the age composition of the samples, since age structure and reporting varied widely across studies. The use of samples with different age composi-

TABLE 1. Geographic distribution of male and female samples¹

Geographic region	Number of samples	
	Males	Females
Sub-Saharan Africa	30	23
North Africa	5	4
Europe	24	19
West Asia	10	5
South Asia	27	8
East Asia	4	4
New Guinea	2	2
Total	102	65

¹ The complete listing of samples is given in the Appendix.

tion should have only minimal effect, since age-related changes in skin color are minor relative to intercontinental populational comparisons.

Samples were assigned geographic coordinates according to their place of origin (e.g., students measured in another country were assigned to their place of origin). The exact location of each local population was determined when possible or extrapolated from a nearby landmark. For less clearly defined regional or national populations, the approximate geographic center was used. The geographic coordinates for each sample were obtained from the original papers, a standard gazetteer (Fullard and Darby, 1969), the Encyclopaedia Britannica (1988), or Hiernaux (1977). Latitude (in degrees and minutes) was converted to a decimal scale, using positive values for the Northern Hemisphere values and negative values for the Southern Hemisphere.

The final data set consists of 102 male samples and 65 female samples, collectively representing skin reflectance data (EEL 609) on 16,104 individuals. A rough geographic breakdown of these samples is given in Table 1. The full listing of samples and references is provided in the Appendix. The complete data listing is available in micro-computer format upon request.

METHODS

The relationship between human skin color and latitude is investigated using a nonlinear piecewise regression. Piecewise regression is a method that joins two or more linear regressions. The model used here is

$$y = a - bx + (2b + c)(x - d)(x > d) \quad (1)$$

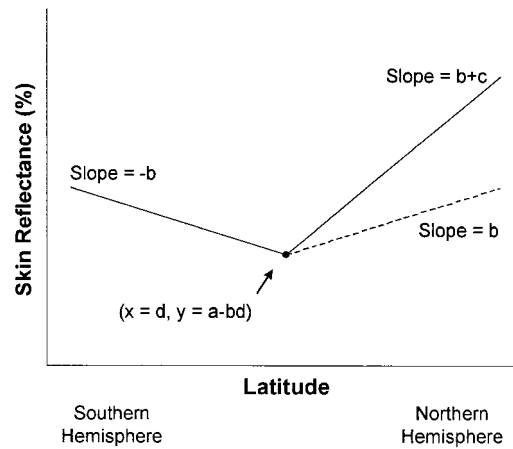


Fig. 1. Graphic presentation of the nonlinear piecewise regression model (equation 1): $y = a - bx + (2b + c)(x - d)(x > d)$, where y is skin reflectance (%) and x is latitude (positive values in the Northern Hemisphere and negative values in the Southern Hemisphere). The relational function $(x > d)$ is equal to 1 when true and 0 when false. Minimum skin reflectance occurs at the point defined by $x = d$ and $y = a - bd$. The parameter b is the slope for the Southern Hemisphere, and $b + c$ is the slope for the Northern Hemisphere. If $c = 0$, then the absolute slopes in the Northern Hemisphere (shown by the dotted line) would be the same as the absolute slope in the Southern Hemisphere. Thus, c is a measure of the hemispheric difference in slopes if $d = 0$ (see text).

where y is skin reflectance and x is latitude. The relational function $(x > d)$ is equal to 1 when true and 0 when false. For values of x that are less than or equal to d , equation 1 reduces to

$$y = a - bx \quad (2)$$

For values of x greater than d equation 1 reduces to

$$y = a - d(2b + c) + (b + c)x \quad (3)$$

Thus, equation 1 describes two linear regressions that meet at point $x = d$ (where both have the value of $y = a - bd$). For $x \leq d$, the linear regression has an intercept of a and a slope of $-b$. For $x > d$, the linear regression has an intercept of $a - d(2b + c)$ and a slope of $b + c$. Figure 1 illustrates the general form of the piecewise regression model.

The parameters of this model allow specific tests of the relationship between latitude and skin reflectance. The parameter d is the latitude at which the two linear regressions (equations 2 and 3) intersect and is the

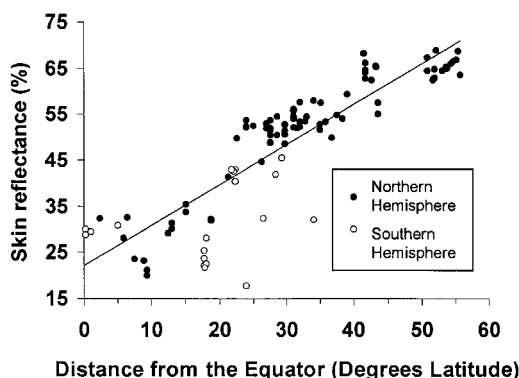


Fig. 2. Linear regression of skin reflectance on distance from the equator (degrees latitude) for 102 male samples ($R^2 = 0.77$). Individual data points are labeled by hemisphere, clearly showing the tendency for samples in the Southern Hemisphere to be darker than those in the Northern Hemisphere at equivalent distance from the equator.

latitude where skin reflectance is at a minimum (and skin color is darkest). Since UV radiation is greatest at the equator, the hypothesized value of d is zero. The parameter b is the absolute value of the slope for values of $x \leq d$. If $d = 0$, then b is the absolute value of the slope in the Southern Hemisphere and $b + c$ is the absolute value of the slope in the Northern Hemisphere ($x > 0$). If there is no hemispheric difference in skin color then the absolute values of the two slopes will be equal ($b = b + c$), or $c = 0$. If $c \neq 0$, then a hemispheric difference exists in skin color. In this case, a positive value of c indicates lower skin reflectance in the Southern Hemisphere, and a negative value of c indicates lower skin reflectance in the Northern Hemisphere. This general model includes the traditional regression model used in skin color research, $y = a + b|x|$ (Roberts and Kahlon, 1976; Tasa et al., 1985), as a subset when $b \neq 0$, $c = 0$, and $d = 0$.

All analyses were performed separately on the male and female data sets. All computations were performed using SYSTAT for Windows, version 6 (SPSS, 1996).

RESULTS

For preliminary investigation, linear regressions of skin reflectance on distance from the equator were performed on both the male and female data sets. Figure 2 shows the scattergram for the male data

TABLE 2. Parameter estimates, standard errors, and 95% confidence intervals for the full model (equation 1)¹

Sex	Parameter	Estimate	SE	95% confidence interval
Male ($R^2 = 0.847$)	a	26.928	2.596	21.777, 32.078
	b	0.268	0.130	0.011, 0.525
	c	0.564	0.138	0.291, 0.837
	d	1.737	2.912	-4.042, 7.515
	$b + c$	0.832	0.046	0.740, 0.923
Female ($R^2 = 0.846$)	a	28.128	3.613	20.903, 35.353
	b	0.367	0.170	0.028, 0.706
	c	0.464	0.180	0.105, 0.824
	d	2.791	3.840	-4.887, 10.470
	$b + c$	0.832	0.060	0.712, 0.951

¹ The model fits the four parameters (a, b, c, d) in equation 1. The slopes for the Northern Hemisphere ($b + c$) and their standard errors are also given, computed as described by Engleman and Wilkinson (1996).

along with the fitted regression line ($R^2 = 0.770$). This graph shows clearly that samples from the Northern Hemisphere tend to lie above the regression line while samples from the Southern Hemisphere tend to lie below the regression line. This result suggests a strong hemispheric component in human skin color variation, with lower reflectances (darker skin) in the Southern Hemisphere. The female data (not shown) ($R^2 = 0.801$) show the same pattern.

Parameter estimates for the full model (equation 1) are reported in Table 2, along with their standard errors and their 95% confidence intervals. A rough measure of goodness of fit, R^2 , was obtained as the square of the correlation between observed and expected values, which is preferred over traditional computations of R^2 in nonlinear regression (Engleman and Wilkinson, 1996). The fit is $R^2 = 0.847$ for the males and $R^2 = 0.846$ for the females.

Parameter estimates for both male and female samples are almost identical. The break point (d) for both males and females is not significantly different from zero, supporting the hypothesis that skin color is darkest at the equator. All other parameter values are large relative to their standard errors, and have confidence intervals that do not include the null hypothesis of zero.

These results suggest that a reduced model, setting $d = 0$, is more appropriate. This hypothesis was tested using an F test for comparing reduced and full models (Engleman and Wilkinson, 1996). The reduced model is not significantly different from the full model for either males

TABLE 3. Parameter estimates, standard errors, and 95% confidence intervals for the reduced model where $d = 0$ (equation 4)¹

Sex	Parameter	Estimate	SE	95% confidence interval
Male ($R^2 = 0.846$)	a	25.561	1.380	22.823, 28.299
	b	0.327	0.087	0.154, 0.500
	c	0.490	0.070	0.352, 0.629
	$b + c$	0.818	0.040	0.738, 0.897
Female ($R^2 = 0.845$)	a	25.771	1.958	21.857, 29.684
	b	0.468	0.108	0.252, 0.685
	c	0.340	0.081	0.178, 0.502
	$b + c$	0.808	0.051	0.706, 0.911

¹ The model fits the three parameters (a , b , c) in equation 4. The slopes for the Northern Hemisphere ($b + c$) and their standard errors are also given, computed as described by Engelman and Wilkinson (1996).

($F = 0.39$, $df = 1$ and 98 , $P = 0.535$) or females ($F = 0.60$, $df = 1$ and 61 , $P = 0.440$). The R^2 values for the reduced model are virtually the same as for the full model (males = 0.846, females = 0.845). The reduced model ($d = 0$) is

$$y = a - bx + (2b + c)x(x > 0). \quad (4)$$

Here the three parameters have direct interpretations: a is the expected skin reflectance at the equator, b is the slope for the Southern Hemisphere, ($b + c$) is the slope for the Northern Hemisphere, and c is a measure of the differences in the slopes.

The results of the nonlinear regression for the reduced model are reported in Table 3. Again, male and female results are virtually the same. The parameter estimates are large relative to their standard errors, and none of the confidence intervals include zero. All F tests for further model reduction ($b = d = 0$, $c = d = 0$, $b = c = d = 0$) are highly significant ($P < 0.001$) for both males and females. The best fitting model is therefore the reduced model in equation 4. The fit of the reduced model is shown in Figure 3 for males and Figure 4 for females.

A final set of analyses was performed to determine if there was any significant effect of longitude by adding longitude as a covariate in equation 4. The longitudinal effect was not significant for either the male or female samples.

DISCUSSION

Previous analyses of the relationship of skin color and latitude have used a simple model where skin reflectance is regressed on distance from the equator. This approach

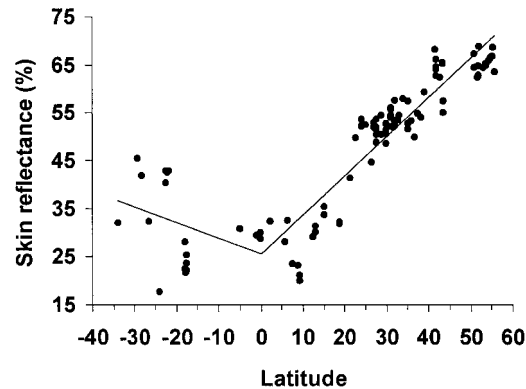


Fig. 3. Nonlinear piecewise regression results for 102 male samples ($R^2 = 0.85$) using the reduced model (equation 4, where $d = 0$): $y = a - bx + (2b + c)x(x > 0)$, where y is skin reflectance (%) and x is latitude (positive values in the Northern Hemisphere and negative values in the Southern Hemisphere). The relational function ($x > 0$) is equal to 1 when true (Northern Hemisphere) and 0 when false (Southern Hemisphere). The regression line for the Southern Hemisphere reduces to $y = a - bx$, and the regression line for the Northern Hemisphere reduces to $y = a + (b + c)x$. Parameter estimates are given in Table 3.

makes two assumptions. The first assumption is that skin reflectance is lowest at the equator. The results of the present study support this assumption ($d = 0$). The second assumption is that the relationship between skin reflectance and latitude is the same in

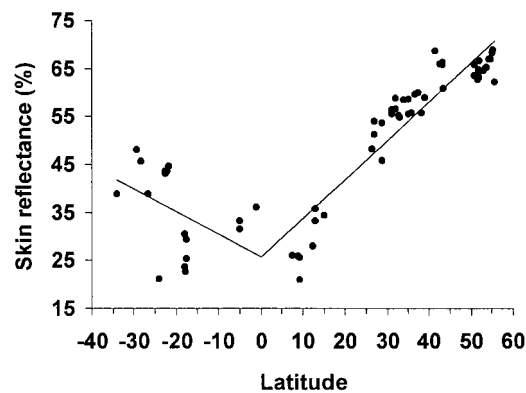


Fig. 4. Nonlinear piecewise regression results for 65 female samples ($R^2 = 0.85$) using the reduced model (equation 4, where $d = 0$): $y = a - bx + (2b + c)x(x > 0)$, where y is skin reflectance (%) and x is latitude (positive values in the Northern Hemisphere and negative values in the Southern Hemisphere). The relational function ($x > 0$) is equal to 1 when true (Northern Hemisphere) and 0 when false (Southern Hemisphere). The regression line for the Southern Hemisphere reduces to $y = a - bx$, and the regression line for the Northern Hemisphere reduces to $y = a + (b + c)x$. Parameter estimates are given in Table 3.

both the Northern and Southern Hemispheres; the present study rejects this hypothesis. The absolute slope of reflectance is lower in the Southern Hemisphere than in the Northern Hemisphere. For both males and females, skin reflectance is lowest at the equator. For every 10 degrees of south latitude (below the equator), skin reflectance increases roughly 3.3% in males and 4.7% in females. For every 10 degrees of north latitude, skin reflectance increases roughly 8.2% in males and 8.1% in females.

A hemispheric difference in the relationship between skin reflectance and latitude is expected given recent findings of higher UV radiation levels in the Southern Hemisphere than in the Northern Hemisphere at equivalent latitude (McKenzie and Elwood, 1990; McKenzie, 1991; Seckmeyer and McKenzie, 1992). If human skin color variation corresponds to variation in UV radiation, then skin reflectances in the Southern Hemisphere will be lower (darker) than those in the Northern Hemisphere at the same distance from the equator. If so, then regressions of skin reflectance on latitude should share the same intercept (the equator) but have different slopes, a prediction confirmed by the present study.

The interpretation of hemispheric differences in UV radiation underlying a hemispheric difference in skin color may not be that straight forward because the factors producing the former have varied over time. The hemispheric difference in UV radiation observed today is due to a number of factors, including ozone concentration, atmospheric turbidity, and the distance of the earth to the sun (McKenzie and Elwood, 1990). If these factors varied in the past, then the present hemispheric difference in UV radiation might have been different in the past. This is certainly the case for the earth-sun distance. At present, the earth is closest to the sun on January 3, corresponding to summer months in the Southern Hemisphere. The earth's orbit has a substantial effect on UV radiation. For example, McKenzie and Elwood (1990) report that UV radiation is roughly 13 percent greater at 45°S than at 45°N, and that roughly half of this difference can be attributed to elliptical orbit (the other half is due to hemispheric asymmetry in ozone

distribution). However, the timing of minimum earth-sun distance (perihelion) changes over time with a period of roughly 26,000 years (Baugher, 1988). Thus, at some points in the past perihelion occurred during the Northern Hemisphere summer. Past seasonal and latitudinal variation in UV radiation would have also been affected by changes in the obliquity of the earth's axis, which has a period of roughly 41,000 years (Baugher, 1988). These cycles interact to produce complicated changes in received solar radiation over time and space.

The interaction of orbital periods and the subsequent effect on received solar radiation and climate are often considered as causal factors for explaining Pleistocene ice ages (Imbrie and Imbrie, 1979, 1980; Baugher, 1988). For the purpose of the present study, such work indicates that *current* conditions have applied at *some* points in our past, but not all. While it is tempting to suggest that there is a direct link between hemispheric variation in UV radiation and skin color, we would need to know the time and rate of skin color evolution relative to the past distribution of UV radiation, which is not possible. The best we can do is suggest the possibility that hemispheric differences in UV radiation *may* have contributed to hemispheric differences in skin color. The distribution of skin color in the world today suggests that human skin color may have evolved primarily during a period of higher aggregate Southern Hemisphere UV radiation. Further analysis of other traits presumably related to UV radiation, such as vitamin-D binding protein allele *GC*1F* (Kamboh and Ferrell, 1986; Szathmary, 1987), may help confirm this hypothesis.

ACKNOWLEDGMENTS

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APPENDIX. References for skin reflectance data

Region	Population ¹	Reference
Sub-Saharan Africa	Adi-Arkai, Ethiopia (MF)	Harrison et al. (1969)
	Central San (MF)	Tobias (1961)
	Central San, Ghanzi (MF)	Weiner et al. (1964)
	Central San, Lone Tree (MF)	Weiner et al. (1964)
	Central San, Takashwani (MF)	Weiner et al. (1964)
	Chopi, Mozambique (MF)	Weninger (1969)
	Congo (MF)	Van Rijn-Tournel (1966)
	Debarech, Ethiopia (MF)	Harrison et al. (1969)
	Dogon (MF)	Huizinga (1968)
	Fali Kangou, Cameroun (MF)	Rigters-Aris (1973b)
	Fali Tinguelin, Cameroun (MF)	Rigters-Aris (1973b)
	Ibo, Nigeria (M)	Barnicot (1958)
	Kenya (M)	Sunderland (1979)
	Khoikhoi, Steinkopf (MF)	Weiner et al. (1964)
	Khoikhoi, Warmbad (MF)	Weiner et al. (1964)
	Kuangali Bantu, Kakura (M)	Weiner et al. (1964)
	Kuangali Bantu, Kurungkuru (MF)	Weiner et al. (1964)
	Kuangali Bantu, Mazua (MF)	Weiner et al. (1964)
	Kuangali Bantu, Tordoro (MF)	Weiner et al. (1964)
	Kuramba, Roanga, Upper Volta (MF)	Huizinga (1968)
	Kwengo (MF)	Weiner et al. (1964)
	M'Bukushu Bantu, Bagani Kraal (MF)	Weiner et al. (1964)
	Nigeria (M)	Ojikutu (1965)
	Oto Ekonda, Zaire (M)	Hiernaux (1976)
	Sara Madjingay, Ndila, Chad (MF)	Hiernaux (1972)
	Sudan (M)	Sunderland (1979)
	Swazi, South Africa (MF)	Roberts et al. (1986)
	Twa Ekonda, Zaire (M)	Hiernaux (1976)
	Xhosa (MF)	Wassermann and Heyl (1968)
North Africa	Yoruba, Nigeria (MF)	Barnicot (1958)
	Chaouias, Algeria (MF)	Chamla and Demoulin (1978)
	Cyrenaica, Libya (MF)	Sunderland (1979)
	Lebanon (MF)	Sunderland (1979)
	Morocco (M)	Sunderland (1979)
Europe	Tripoli, Libya (MF)	Sunderland (1979)
	Ballinlough, Ireland (MF)	Sunderland et al. (1973)
	Basque, Ancares, Spain (MF)	Rebato (1987)
	Basque, Guipuzcoa, Spain (MF)	Rebato (1987)
	Basque, Vizcaya, Spain (MF)	Rebato (1987)
	Bierzo, Spain (M)	Caro (1980)
	Brussels, Belgium (MF)	Leguebe (1961)
	Brussels, Belgium (MF)	Van Rijn-Tournel (1966)
	Cabera, Spain (M)	Caro (1980)
	Carnew, Ireland (MF)	Sunderland et al. (1973)
	Cumberland, England (MF)	Smith and Mitchell (1973)
	Holy Island, Northumberland (MF)	Cartwright (1975)
	Isle of Man (MF)	Smith and Mitchell (1973)
	Longford, Ireland (MF)	Unpublished data ²
	Maragateria, Spain (M)	Caro (1980)
	Merthyr Tydfil, Wales (MF)	Smith and Mitchell (1973)
	Mesata, Spain (M)	Caro (1980)
	Montana, Spain (M)	Caro (1980)
	North Northumberland, England (MF)	Hulse (1973)
	North Pembrokeshire, Wales (MF)	Sunderland and Wooley (1982)
	Rossmore, Ireland (MF)	Sunderland et al. (1973)
	Sanabria, Spain (MF)	Rebato (1987)
	South Pembrokeshire, Wales (MF)	Sunderland and Wooley (1982)
	Southeast Northumberland, England (MF)	Hulse (1973)
West Asia	Utrecht, Netherlands (MF)	Rigters-Aris (1973a)
	Arabia (M)	Sunderland (1979)
	Chechen (M)	Sunderland (1979)
	Druze, Syria (M)	Sunderland (1967)
	Israeli Arabs (MF)	Sunderland (1979)
	Jordan (M)	Sunderland (1979)
	Jordanian Arabs (M)	Sunderland (1967)
	Kurdistan (MF)	Sunderland (1979)
	Nowshahr City, Iran (MF)	Mehrai and Sunderland (1990)
	Turkey (MF)	Sunderland (1979)
	Yemenite Jews, Israel (MF)	Hulse (1969)

(Continued)

APPENDIX. References for skin reflectance data (continued)

Region	Population ¹	Reference
South Asia	Aggami Nagas, India (MF)	Set and Set (1978)
	Arora, North India (MF)	Kalla (1969)
	Bado Gadaba, India (M)	Das and Mukherjee (1963)
	Baniyas, North India (M)	Jaswal (1979)
	Bareng Paroja, India (M)	Das and Mukherjee (1963)
	Bengali Brahmins, India (M)	Tiwari (1963)
	Bengali Kayastha, India (M)	Tiwari (1963)
	Bengali Vaidya, India (M)	Tiwari (1963)
	Brahman, Nepal (M)	Williams-Blangero and Blangero (1991)
	Brahman, North India (M)	Jaswal (1979)
	Chetri, Nepal (M)	Williams-Blangero and Blangero (1991)
	Haryam Jats, North India (M)	Jaswal (1979)
	Jat Sikhs, North India (M)	Jaswal (1979)
	Jirel, Nepal (M)	Williams-Blangero and Blangero (1991)
	Khatri, North India (M)	Jaswal (1979)
	Khatri, North India (MF)	Kalla (1969)
	Mahar, India (M)	Das and Mukherjee (1963)
	Pakistan (MF)	Sunderland (1979)
	Punjabi, India (MF)	Banerjee (1984)
	Rajputs, North India (M)	Jaswal (1979)
	Rarhi Brahman, India (M)	Das and Mukherjee (1963)
	Saxena Kayastha, India (MF)	Kalla (1972)
	Sherpa, Nepal (M)	Williams-Blangero and Blangero (1991)
	Sihks, India (MF)	Kahlon (1973)
	Sunwar, Nepal (M)	Williams-Blangero and Blangero (1991)
	Tamang, Nepal (M)	Williams-Blangero and Blangero (1991)
	Tibet (MF)	Kalla and Tiwari (1970)
East Asia	Ainu, Japan (MF)	Harvey and Lord (1978)
	Central Japan (MF)	Hulse (1967)
	Northern Japan (MF)	Hulse (1967)
	Southwest Japan (MF)	Hulse (1967)
New Guinea	Karkar Island, Papua New Guinea (MF)	Harvey (1985)
	Lufa, Papua New Guinea (MF)	Harvey (1985)

¹ M, male; F, female.

² This skin color study was described by Lees et al. (1979) and Relethford et al. (1985), but means for males and females were not previously reported and are given here for the EEL 609 filter. Males: N = 312, \bar{X} = 64.91, SD = 2.75; females: N = 39, \bar{X} = 65.21, SD = 2.39.

LITERATURE CITED

- Banerjee S (1984) The inheritance of constitutive and facultative skin colour. *Clin. Genet.* 25:256–258.
- Barnicot NA (1958) Reflectometry of the skin in southern Nigerians and in some mulattoes. *Hum. Biol.* 30:150–160.
- Baughner JF (1988) *The Space Age Solar System*. New York: John Wiley.
- Blum HF (1969) Is sunlight a factor in the geographic distribution of human skin color? *Geog. Rev.* 59:557–581.
- Byard PJ (1981) Quantitative genetics of human skin color. *Yrbk. Phys. Anthropol.* 24:123–137.
- Caro L (1980) La reflectancia de la piel en Espanoles del Noroeste. *Bol. De la Soc. Esp. de Antropologia Biologica* 1:24–31.
- Cartwright RA (1975) Skin reflectance results from Holy Island, Northumberland. *Ann. Hum. Biol.* 2:347–354.
- Chamla MC, and Demoulin F (1978) Reflectance de la peau, pigmentation des cheveux et des yeux des Chaouis de Bouzina (Aures, Algeria). *L'Anthropologie* 82:61–94.
- Das SR, and Mukherjee DP (1963) A spectrophotometric skin colour survey among four Indian castes and tribes. *Z. Morphol. Anthropol.* 54:190–200.
- Encyclopaedia Britannica (1988) *Encyclopaedia Britannica*. Chicago: Encyclopaedia.
- Engelman L, and Wilkinson L (1996) Nonlinear regression. In *Statistics: SYSTAT 6.0 for Windows*. Chicago: SPSS, Inc., pp. 447–496.
- Frisancho AR (1993) *Human Adaptation and Accommodation*. Ann Arbor: University of Michigan Press.
- Fullard H, and Darby HC (eds.) (1969) *Aldine University Atlas*. Chicago: Scott, Foresman and Co.
- Garrard G, Harrison GA, and Owen JJ (1967) Comparative spectrophotometry of skin colour with EEL and Photovolt instruments. *Am. J. Phys. Anthropol.* 27: 389–396.
- Harrison GA, Kuchemann CF, Moore MAS, Boyce AJ, Bajaj T, Mourant AE, Godber MJ, Glasgow BG, Kopec AC, and Tills D (1969) The effects of altitudinal variation in Ethiopian populations. *Philos. Trans. R. Soc. Lond. [Biol.]* 256:147–182.
- Harvey RG (1985) Ecological factors in skin color variation among Papua New Guineans. *Am. J. Phys. Anthropol.* 66:407–416.
- Harvey RG, and Lord JM (1978) Skin colour of the Ainu of Hidaka, Hokkaido, Northern Japan. *Ann. Hum. Biol.* 5:459–467.
- Hiernaux J (1972) La reflectance de la peau dans une commune de Sara Madjingay (Republique du Tchad). *L'Anthropologie* 76:279–300.
- Hiernaux J (1976) Skin color and climate in central Africa: A comparison of three populations. *Hum. Ecol.* 4:69–73.

- Hiernaux J (1977) Long-term biological effects of human migration from the African savanna to the equatorial forest: A case study of human adaptation to a hot and wet climate. In GA Harrison (ed.): *Population Structure and Human Variation*. London: Cambridge University Press, pp. 187–217.
- Huizinga J (1968) Human biological observations on some African populations of the thorn savanna belt. I. *Proc. Koninkl. Neder. Akademie van Wetenschappen (Series C)* 71:356–372.
- Hulse FS (1967) Selection for skin color among the Japanese. *Am. J. Phys. Anthropol.* 27:143–156.
- Hulse FS (1969) Skin color among the Yemenite Jews of the isolate from Habban. *Proc. 8th Cong. Anthropol. Ethnol. Sci. (Tokyo)*, pp. 226–228.
- Hulse FS (1973) Skin colour in Northumberland. In DF Roberts and E Sunderland (eds.): *Genetic Variation in Britain*. London: Taylor and Francis, pp. 245–257.
- Imbrie J, and Imbrie KP (1979) *Ice Ages: Solving the Mystery*. Short Hills, NJ: Enslow Publishers.
- Imbrie J, and Imbrie JZ (1980) Modeling the climatic response to orbital variations. *Science* 207:943–953.
- Jaswal IJS (1979) Skin color in North Indian populations. *J. Hum. Evol.* 8:361–366.
- Kahlon DPS (1973) Skin colour in the Sikh community in Britain. In DF Roberts and E Sunderland (eds.): *Genetic Variation in Britain*. London: Taylor and Francis, pp. 141–159.
- Kalla AK (1969) Affinities in skin pigmentation of some Indian populations. *Hum. Hered.* 19:499–505.
- Kalla AK (1972) Parent-child relationship and sex differences in skin tanning potential in man. *Humangenetik* 15:39–43.
- Kalla AK, and Tiwari SC (1970) Sex differences in skin colour in man. *Acta. Genet. Med. Gemellol.* 19:472–476.
- Kamboh MI, and Ferrell RE (1986) Ethnic variation in vitamin D-binding protein (GC): A review of isoelectric focusing studies in human populations. *Hum. Genet.* 72:281–293.
- Lees FC, and Byard PJ (1978) Skin colorimetry in Belize. I. Conversion formulae. *Am. J. Phys. Anthropol.* 48:515–522.
- Lees FC, Byard PJ, and Relethford JH (1978) Interobserver error in human skin colorimetry. *Am. J. Phys. Anthropol.* 49:35–38.
- Lees FC, Byard PJ, and Relethford JH (1979) New conversion formulae for light-skinned populations using Photovolt and E.E.L. reflectometers. *Am. J. Phys. Anthropol.* 51:403–408.
- Leguebe A (1961) Contribution a l'etude de la pigmentation chez l'homme. *Institut royal des Sciences naturelles de Belgique* 37:1–29.
- Loomis WF (1967) Skin-pigment regulation of vitamin-D biosynthesis in man. *Science* 157:501–506.
- McKenzie RL (1991) Application of a simple model to calculate latitudinal and hemispheric differences in ultraviolet radiation. *Weather and Climate* 11:3–14.
- McKenzie RL, and Elwood JM (1990) Intensity of solar ultraviolet radiation and its implications for skin cancer. *N. Z. Med. J.* 103:152–154.
- Mehrai H, and Sunderland E (1990) Skin colour data from Nowshahr City, Northern Iran. *Ann. Hum. Biol.* 17:115–120.
- Ojikutu RO (1965) Die rolle von hautpigment und schwebdrusen in der klimannpassung des menschen. *Homo* 16:77–95.
- Rebato E (1987) Skin colour in the Basque populations. *Anthropol. Anz.* 45:49–55.
- Relethford JH, Lees FC, and Byard PJ (1985) Sex and age variation in the skin color of Irish children. *Curr. Anthropol.* 26:396–397.
- Rigters-Aris CAE (1973a) A reflectometric study of the skin in Dutch families. *J. Hum. Evol.* 2:123–136.
- Rigters-Aris CAE (1973b) Reflectometrie cutanee des Fali (Cameroun). *Proc. Koninkl. Nederl. Akademie van Wetenschappen, (Series C)* 76:500–511.
- Roberts DF, and Kahlon DPS (1976) Environmental correlations of skin colour. *Ann. Hum. Biol.* 3:11–22.
- Roberts DF, Kromberg JG, and Jenkins T (1986) Differentiation of heterozygotes in recessive albinism. *J. Med. Genet.* 23:323–327.
- Robins AH (1991) *Biological Perspectives on Human Pigmentation*. Cambridge: Cambridge University Press.
- Seckmeyer G, and McKenzie RL (1992) Increased ultraviolet radiation in New Zealand (45°S) relative to Germany (48°N). *Nature* 359:135–137.
- Set PV, and Set S (1978) Physical anthropology of the Angami Nagas (Nagaland, India). In RJ Meier, CM Otten, F Abdel-Hameed (eds.): *Evolutionary Models and Studies in Human Diversity*. Paris: Mouton, pp. 325–332.
- Smith J, Mitchell RJ (1973) Skin colour studies in South Wales, the Isle of Man, and Cumbria. In DF Roberts and E Sunderland (eds.): *Genetic Variation in Britain*. London: Taylor and Francis, pp. 259–264.
- SPSS (1996) *Systat 6.0 for Windows*. Chicago: SPSS, Inc.
- Sunderland E (1967) The skin colour of the people of Azraq, eastern Jordan. *Hum. Biol.* 39:65–70.
- Sunderland E (1979) Skin color variability in the Middle East and Asia. In WA Stini (ed.): *Physiological and Morphological Adaptation and Evolution*. Paris: Mouton, pp. 7–18.
- Sunderland E, Tills D, Bouloux C, and Doyl J (1973) Genetic studies in Ireland. In DF Roberts and E Sunderland (eds.): *Genetic Variation in Britain*. London: Taylor and Francis, pp. 141–159.
- Sunderland E, and Wooley V (1982) A study of skin pigmentation in the population of the former county of Pembrokeshire, Wales. *Hum. Biol.* 54:387–401.
- Szathmary EJE (1987) The effect of GC genotype on fasting insulin level in Dogrib Indians. *Hum. Genet.* 75:368–372.
- Tasa GL, Murray CJ, and Boughton JM (1985) Reflectometer reports on human pigmentation. *Curr. Anthropol.* 26:511–512.
- Tiwari SC (1963) Studies of crossings between Indians and Europeans. *Ann. Hum. Genet.* 26:219–227.
- Tobias PV (1961) Studies in skin reflectance in Bushman-European hybrids. *Proc. Int. Congress Hum. Genet., 2nd meeting*, pp. 461–471.
- Van Rijn-Tournel J (1966) Pigmentation de la peau de Belges et D'Africains. *Bull. Soc. Roy. Belge Anthropol. Prehist.* 76:79–96.
- Wassermann HP, and Heyl T (1968) Quantitative data on skin pigmentation in South African races. *S. A. Med. J.* 42:98–101.
- Weiner JS (1951) A spectrophotometer for measurement of skin color. *Man* 51:152–153.
- Weiner JS, Harrison GA, Singer R, Harris R, and Jopp W (1964) Skin colour in southern Africa. *Hum. Biol.* 36:294–307.
- Weninger M (1969) Spektrophotometrie untersuchungen der Haut an einem Bantu-Stamm (Chope) aus Mocambique. *Anthropologie* 7:53–58.
- Williams-Blangero S, and Blangero J (1991) Skin color variation in eastern Nepal. *Am. J. Phys. Anthropol.* 85:281–291.